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A review of Hyposoter parasitoid wasps (Hymenoptera, Ichneumonidae) in Switzerland

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Abstract

Darwin wasps represent the most species-rich family of parasitoid wasps but remain strongly understudied, with many species yet to be formally described. This is especially the case for the subfamily Campopleginae, a group of koinobiont endoparasitoids of various holometabolan insect orders. We studied most Campopleginae specimens housed at three major Swiss natural history collections, including 1,046 specimens of *Hyposoter*. We identified 53 of the 71 Western Palaearctic *Hyposoter* species in Switzerland, including 46 first records, one of which we describe as a new species. Using abundance-based coverage estimators, we estimate 54–61 *Hyposoter* species in the country. We show that the genus is more species-rich at low altitude and that only three species can be considered as high-altitude specialists, as many show broad altitudinal ranges. We describe *Hyposoter beaumonti* **sp. nov.** from Western Switzerland and establish three new synonyms: *Hyposoter monensis* Galsworthy & Shaw, 2023 of *Phobocampe nigra* Sedivy, 2004 (**syn. nov.**), the former becoming the valid name because the latter becomes a secondary homonym of *Hyposoter niger* (Brullé, 1846), *Hyposoter castaneus* Galsworthy & Shaw, 2023 of *Lemophagus curtus* Townes, 1965 (**syn. nov.**), and *Hyposoter caedator corsicator* Aubert, 1960 of *Hyposoter caedator* (Gravenhorst, 1829) (**syn. nov.**). Our findings underscore the critical role of diversified sampling strategies—including along altitudinal gradients—and up-to-date taxonomic revisions. They also highlight the importance of digitizing and publishing collection data after accurate identification, thereby enhancing the accessibility of ecological and biological information stored in natural history collections for future research.

Key Words

Biodiversity, checklist, collection effort, faunistics, host records, new taxa, phenology, species accumulation curve

Introduction

Biogeographic patterns in Darwin wasps

Darwin wasps (Ichneumonidae) are the largest family of parasitoid wasps (Aguiar et al. 2013; Yu et al. 2016[1]). They remain severely understudied across most regions of the world (Klopfstein et al. 2019b), with substantial differences between the relatively better-studied temperate regions and the poorly studied tropics, which partly obscures our understanding of this family's biogeographic patterns (Quicke 2012). While diversity patterns of ichneumonids along latitudinal gradients have been discussed controversially (Owen and Owen 1974; Quicke 2012; Timms et al. 2016; Santos et al. 2025), altitudinal patterns have received relatively little

1 The database is officially unavailable, but many copies are circulating.

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attention (Veijalainen et al. 2013; Timms et al. 2016). According to studies from the Neotropics, Darwin wasps have a strong turnover along altitudinal gradients (Veijalainen et al. 2014; Higa and Penteado-Dias 2020; Flinte et al. 2023), while a trend in species richness along the altitudinal gradient seems to be less consistent (Veijalainen et al. 2014; Higa and Penteado-Dias 2020; Flinte et al. 2023). In the Western Palaearctic, regions at higher elevation are not only rather species-rich in Darwin wasps, but also much less intensively studied compared to localities at lower elevation and thus likely harbour a large proportion of the still undescribed diversity (Schwarz 2002; Klopfstein et al. 2007; Klopfstein 2014; Johansson 2024).

Darwin wasp diversity in Switzerland

Switzerland is 58% covered by the Alps, 11% by the Jura mountains and 31% by the central plateau (Swiss Confederation 2023). Therefore, it provides excellent preconditions to study altitudinal patterns (e.g., Wigger et al. 2015; Gilgado et al. 2022). Although the flora and fauna are relatively well studied in Switzerland, the inventory of several insect groups is still far from complete (Baur and Ungricht 2019; Widmer et al. 2021). Baur and Ungricht (2019) estimate that only between 32–65% of Diptera and around 45% of Hymenoptera species expected to be present have been recorded in Switzerland. Among Hymenoptera, parasitoid wasps clearly make up the largest part of the so far unrecorded species (Baur and Ungricht 2019), an observation mirrored in large insect inventories in Canada and Sweden (Hebert et al. 2016; Ronquist et al. 2020). A preliminary checklist of Darwin wasps based on major Swiss collections (Klopfstein et al. 2019a) included 1,878 species, but emphasized that the Swiss fauna of Darwin wasps is still poorly studied, both in terms of reliable species identifications and of the coverage of sampled habitats. It is likely that the actual species richness of Darwin wasps in Switzerland is comparable to that of more intensively studied countries in central Europe, such as Germany with 3,644 species (Riedel et al. 2021). The publication of 15 additional species for Switzerland since 2019 indicates that many of the so far undetected species can be found in the unidentified material of Swiss natural history collections (N = 3, Meier et al. 2022; N = 1, Galsworthy 2023; N = 6, Perret-Gentil et al. 2024; N = 4, Johansson 2024; N = 1, Urfer et al. 2025). In order to tackle these shortcomings, Swiss natural history collections have recently been complemented by specimens collected with Malaise trap projects from various localities (both at high and low altitudes). Funding from the Swiss government via the "SwissCollNet" program allowed us to properly identify Darwin wasp specimens of the very diverse and poorly studied subfamily Campopleginae.

The genus *Hyposoter*

Hyposoter Förster, 1869 is one of the top five most species-rich genera of Campopleginae, with 147 described species worldwide (GBIF 2025) and 71 species in the Western Palaearctic (Galsworthy et al. 2023). Only six species were recorded from Switzerland in the checklist (Klopfstein et al. 2019a), due to unavailability at that time of reliably identified material. Until recently, the identification of *Hyposoter* species was strongly hampered because the only identification key for the European species available was more than 100 years old, incomplete and obscured by synonyms and mistakes (Schmiedeknecht 1909). Recently, Galsworthy et al. (2023) published a new identification key for European *Hyposoter* based on taxonomic notes and the collection of the late Klaus Horstmann, supplemented by the study of other material in the Natural History Museum (London) and the National Museums of Scotland (Edinburgh). This monumental work finally allows reliable species identifications in this diverse genus and reports one more species (*Hyposoter rufonigrator* Galsworthy & Shaw, 2023) from Switzerland.

Hyposoter is morphologically similar to *Phobocampe* Förster, 1869, *Olesicampe* Förster, 1869 and, at least in the male sex, *Diadegma* Förster, 1869, but at least females of the European species can usually be reliably separated using the characters in a recent interactive key (Klopfstein et al. 2022). All species of *Hyposoter* with reliable host information are koinobiont endoparasitoids of lepidopterans from various families (Shaw et al. 2016). They oviposit into early stages of the host larva and kill it prior to pupation (Shaw et al. 2016; Broad et al. 2018). *Hyposoter horticola* Gravenhorst, 1829 is the only species among Campopleginae known to oviposit into the egg of its host, *Melitaea cinxia* (L.) (Van Nouhuys and Kaartinen 2008). Nouhuys and Kaartinen (2008) found that *H. horticola* females revisit the egg clutches of *M. cinxia* to ensure oviposition immediately before the larvae hatch, thus showing a remarkable memory. As most members of the subfamily, many *Hyposoter* species spin their own, bird-dropping-like cocoon after leaving their host. Others spin their cocoon while still inside the larval skin of the caterpillar, obtaining protection through its often setose cuticle or through camouflage (Shaw et al. 2016). Several *Hyposoter* species have proven useful for biological pest control, such as *H. didymator* against the noctuids *Spodoptera littoralis* (Boisduval, 1833) and *S. exigua* (Hübner, 1808) (Morel et al. 2023), and *Hyposoter ebeninus* against *Pieris brassicae* L. and *Pieris rapae* L. (Harvey et al. 2010).

In this study, we use data from 1,046 *Hyposoter* specimens from the natural history collections in Basel, Bern and Lausanne to estimate total species richness and investigate altitudinal patterns in the genus. We examine historical and recent collecting efforts, provide data on phenology, and report rearing records. The checklist of the *Hyposoter* species in Switzerland is complemented by the description of a new species from Western Switzerland.

Materials and methods

Abbreviations of depositories

MZL Naturéum, Muséum cantonal des sciences naturelles, Lausanne (contact : Anne Freitag)
NHMUK Natural History Museum, London, UK (Gavin Broad)
NMBE Naturhistorisches Museum, Bern (Hannes Baur)
NMB Naturhistorisches Museum, Basel (Seraina Klopfstein)
NMS National Museums Scotland, Edinburgh (Ashleigh Whiffin)
ZSM Zoologische Staatssammlung München, Germany (Stefan Schmidt†)

Material

For our faunistic analyses, we studied 1,046 *Hyposoter* specimens from Switzerland (MZL, N = 536; NMB, N = 443; NMBE, N = 67). Of this material, 701 specimens were hand-collected, mostly between 1880 and 1970. No specimens were collected specifically for this study, but a considerable amount of bulk material from recent Malaise trap projects was newly sorted and mounted, yielding 345 Hyposoter specimens. These Malaise trap projects were run by various institutions, such as the Association de la Grande Cariçaie (AGC; N = 58, see for more information about the collection sites in Fisler et al. 2019), Centre Suisse de Cartographie de la Faune (CSCF; N = 188, various contributors) and collection efforts by the NMBE (mostly by Hannes Baur) and the NMB (N = 99, e.g., Klopfstein et al. 2007).

To resolve taxonomic issues and as reference material, we studied specimens (mostly type material) from the NHMUK, NMS and the Horstmann collection (ZSM), including material collected from outside Switzerland.

This work and the included nomenclatural acts are registered in ZooBank (https://www.zoobank.org, accessed on 08 December 2025) under the LSID: https://zoobank.org/AB222E81-5390-480B-81F0-23529141DCD6.

Identification literature and morphological terminology

Hyposoter species were identified using the new identification key (Galsworthy et al. 2023), at times complemented by direct comparison with type material. Morphological terminology follows Broad et al. (2018). The dimensions of the face (excluding the clypeus) were measured from the ventral margin of the antennal sockets to the tentorial pits and as the distance between the inner eye margins at the level of the antennal sockets. The dimensions of the clypeus were measured between the mandibular bases and from the apical margin of the clypeus to the height of the tentorial pits. Images of the specimens were taken with a Keyence VHX-6000 and the VH-Z20R/Z20T lens applying stacking and stitching techniques on single images with 150–200 × magnification. Measurements were made with a Keyence VHX-6000, except for angles that were measured with the software Fiji.

Species richness estimation

We used two non-parametric species richness estimators, Chao-I and the abundance-based coverage estimator, to estimate the number of rare species that have not yet been collected (Chao and Lee 1992; Colwell et al. 2012). The Chao-I estimator estimates the total number of species, including the undetected ones, based on the number of species represented by only one (singletons) or two (doubletons) specimens (Colwell et al. 2012). The abundance-based coverage estimator (ACE) uses by default species with less than 10 specimens as "rare species" and incorporates the proportion of specimens in rare species as well as the variance among rare species in order to estimate the total number of species including so far undetected ones (Chao and Lee 1992). We calculated Chao-I and ACE using the R function vegan::estimateR (Oksanen et al. 2020). Both estimators reported confidence intervals (CI) with a lower bound that is lower than the actual species count, which is not biologically meaningful; we thus truncated the CIs at the observed number.

We checked the results from the species richness estimators visually with species accumulation curves. Species accumulation curves were drawn in two different ways: i) cumulative number of species versus year of collecting; and ii) cumulative number of species versus number of specimens, using 1,000 iterations with random shuffling of the specimens' order.

Testing altitudinal distribution

Whenever possible, we used elevation data from specimen labels (metres above sea level). For the majority of specimens, this information was missing, but where the locality information allowed identification at least of the municipality, we approximated the altitude by calculating mean altitude per municipality with QGIS using zonal statistics on a DHM25 / 200m elevation model and a simple municipality grid. However, we observed that this approximation tends to overestimate the altitude of the sampling locality, especially in montane and alpine municipalities which typically extend up to mountain ridges. Since collectors historically usually reported the name of the village where they collected a sample instead of the political municipality, we corrected samples from

municipalities with mean altitudes above 700 m by manually extracting the altitude of the village. Specimens with inadequate locality information were omitted from the analysis of altitudinal patterns.

Phenology and host records

To examine the phenology of *Hyposoter* species in Switzerland, we filtered out specimens that were reared because of the uncertainty in the meaning of the dates mentioned on the labels without proper prefixes, e.g., such as date of collection of the host larva, pupation date or emergence date of the parasitoid wasp (see also Shaw 2023). Regarding the precision of the date, we allowed for missing years, and approximated missing day values with the 15th as the mid of the month, but discarded specimens from this analysis with missing month values.

We report data for five specimens belonging to five different species with rearing records in our sample. We evaluated these host records based on the history of host records (A), the ecology of the host and the parasitoid (B), the presence of host remains (C), the reliability of the parasitoid identification (D) and the accessibility of the specimen (E) using a 5-digit host record quality code (later just called "code"), following Shaw (2023):

A. Host is same species as host of holotype = 1. Close relative = i. Otherwise 0.
B. Host consistent (phylogeny or ecology) with expectation for parasitoid or its relatives = 1. Insufficient knowledge of parasitoid or its relatives to judge = i. Anomalous = 0.
C. Fully audited rearing (host remains and site of parasitoid's development to adult, e.g. cocoon, host pupa, etc., present) = 1. Deficient in some respects but judged convincing from context (subjective) = i. Substrate rearing = 0.
D. Parasitoid determined by named (or deducible) person at a date during or following last relevant revision = 1. Determined by named person prior to the last revision = i. Otherwise 0.
E. Named accessible repository for parasitoid given = 1. Probable accessible repository easily deduced = i. No repository stated or easily deduced = 0.

Results

Checklist of *Hyposoter* species in Switzerland

We identified the 1,046 studied specimens as 53 species of *Hyposoter* in Switzerland (Table 1). Of these, 46 species are reported for the first time, including *Hyposoter beaumonti* sp. nov., which is newly described in this paper. The complete digitized data of all specimen records are available in Suppl. material 1 and Zenodo (https://doi.org/10.5281/zenodo.17858878).

Hyposoter species richness in Switzerland

In addition to the 53 species recorded here, non-parametric species richness estimators suggest that there is probably at least one more species that has not yet been sampled (Chao-I: 54.2, 95% CI = 53.0–57.8; ACE: 54.4, 95% CI = 53.0–61.3). Even though the difference between the observed and expected species number is relatively small (1.2–1.4), the confidence intervals are quite large, allowing up to 61.3 species (more than 8 so far unrecorded, see violet area in Fig. 1). For comparison, 71 *Hyposoter* species are currently known from Europe (Galsworthy et al. 2023, corrected with results from this study). The prospect that our checklist of Swiss *Hyposoter* might still increase slightly in the future is further supported by the species accumulation curve (Fig. 1a), which has not quite levelled off yet. The species accumulation curve not by specimen, but over the years of collecting (Fig. 1b), well illustrates the intensity and success of collecting efforts over time. The periods of collecting by Theodor Steck (leg. 1880–1930) and Jacques de Beaumont (leg. 1940–1970) are represented as phases of steady species accumulation, with the slope of the latter notably steeper (Fig. 1b, Suppl. material 1). Very few *Hyposoter* specimens were collected in the period 1970–2000, but more recent Malaise trap projects have raised the total number of species significantly between 2000–2020. These Malaise trap projects were run by various institutions and often had a stronger focus on localities at higher elevation (Fig. 1c).

Altitudinal distribution patterns

Most species and specimens of *Hyposoter* in Switzerland were collected below 1,000 m elevation (Fig. 2). A total of 39 species have a median recorded elevation below 1,000 m, 10 species between 1,000–1,500 m, and 3 species above 1,500 m (Fig. 2). We observed that 10 species were collected both below 500 m and above 1,500 m. *Hyposoter caedator* was collected at the lowest altitude, at 270 m in Münchenstein (Basel-Landschaft). *Hyposoter culminator* was collected at the highest altitude at 2,145 m in Alp Flix (Grisons), followed by *Hyposoter sicarius* at 2,100 m in Zernez (Grisons) and a couple of species that were collected at 1,987 m in Alp Flix (Grisons) (Fig. 2). However, altitudinal distributions for 23 species were derived from five or fewer specimens and may therefore deviate from their actual ranges in Switzerland.

We could not find any distinct morphological patterns along the altitudinal distribution gradient, such as darker colouration due to thermal melanism at higher altitudes (Clusella Trullas et al. 2007), or size variation (Hodkinson 2005).

Phenology

The first appearance of *Hyposoter* species in the year is in April and includes *H. leucomerus*, *H. brischkei*, *H. boops*, *H. didymator*, *H. dubitatus*, *H. caedator*

Table 1. Checklist of *Hyposoter* species in Switzerland. Species marked with an asterisk (*) have not previously been recorded in Switzerland (Klopfstein et al. 2019a). The institution acronyms indicate where material of each species is deposited; MZL = Naturéum, Muséum cantonal des sciences naturelles, Lausanne, NMB = Naturhistorisches Museum Basel, NMBE = Naturhistorisches Museum Bern. Literature citations refer to the first record of a species in Switzerland.

Species	Depository	Literature
**Hyposoter aglyphus* Galsworthy & Shaw, 2023	MZL, NMB	
**Hyposoter albonotatus* (Bridgman, 1889)	MZL, NMB, NMBE	
**Hyposoter albosignatus* Galsworthy & Shaw, 2023	MZL, NMB, NMBE	
**Hyposoter alpicola* (Smits van Burgst, 1915)	MZL, NMB	
**Hyposoter barrettii* (Bridgman, 1881)	MZL, NMB	
**Hyposoter beaumonti* sp. nov.	MZL	
**Hyposoter boops* (Thomson, 1887)	MZL, NMB	
**Hyposoter brischkei* (Bridgman, 1882)	MZL, NMB, NMBE	
**Hyposoter caedator* (Gravenhorst, 1829)	MZL, NMB	
**Hyposoter carbonarius* (Ratzeburg, 1844)	NMB	
Hyposoter caudator Horstmann, 2008	MZL, NMBE	(Horstmann 2008)
**Hyposoter clausus* (Brischke, 1880)	MZL, NMB	
**Hyposoter coxator* (Thomson, 1887)	MZL, NMB	
Hyposoter culminator Aubert, 1974	MZL, NMB, NMBE	(Aubert 1980)
Hyposoter didymator (Thunberg, 1824)	MZL, NMB, NMBE	(Artmann-Graf et al. 2009)
**Hyposoter discedens* (Schmiedeknecht, 1909)	MZL, NMB	
**Hyposoter dolosus* (Gravenhorst, 1829)	MZL, NMB, NMBE	
**Hyposoter dubitatus* (Holmgren, 1860)	MZL, NMB	
Hyposoter ebeninus (Gravenhorst, 1829)	MZL, NMB, NMBE	(Blösch 1906)
**Hyposoter ebenitor* Aubert, 1972	MZL	
**Hyposoter fitchii* (Bridgman, 1881)	MZL, NMB	
**Hyposoter flavicoxa* Galsworthy & Shaw, 2023	MZL, NMB	
**Hyposoter heidiella* Galsworthy & Haraldseide, 2023	MZL, NMB	
**Hyposoter horstmanni* Galsworthy & Shaw, 2023	MZL	
**Hyposoter horticola* (Gravenhorst, 1829)	NMB, NMBE	
**Hyposoter inquinatus* (Holmgren, 1860)	MZL, NMB, NMBE	
**Hyposoter insulator* Aubert, 1960	MZL, NMB, NMBE	
**Hyposoter karmensis* Galsworthy & Haraldseide, 2023	MZL, NMB	
**Hyposoter leucomerus* (Thomson, 1887)	MZL, NMB, NMBE	
**Hyposoter longulus* (Thomson, 1887)	MZL, NMB	
**Hyposoter maculatus* (Hedwig, 1938)	MZL, NMB	
**Hyposoter neglectus* (Holmgren, 1860)	MZL, NMB, NMBE	
**Hyposoter nigritus* (Holmgren, 1860)	MZL, NMB	
**Hyposoter notatus* (Gravenhorst, 1829)	MZL, NMB, NMBE	
**Hyposoter orbator* (Gravenhorst, 1829)	NMB	
Hyposoter placidus (Desvignes, 1856)	MZL	(Klopfstein et al. 2019a)
**Hyposoter praecaedator* Aubert, 1963	MZL, NMB, NMBE	
**Hyposoter prolixus* (Holmgren, 1860)	NMB	
**Hyposoter pseudodidymator* Galsworthy & Shaw, 2023	MZL, NMB, NMBE	
Hyposoter rapacitor Aubert, 1971	MZL, NMB, NMBE	(Aubert 1971)
**Hyposoter rhodocerae* (Rondani, 1877)	MZL, NMB	
**Hyposoter rivulator* Galsworthy & Shaw, 2023	MZL, NMB, NMBE	
**Hyposoter ruficoxator* Galsworthy & Shaw, 2023	MZL, NMB	
**Hyposoter ruficrus* (Thomson, 1887)	MZL, NMB, NMBE	
Hyposoter rufonigrator Galsworthy & Shaw, 2023	MZL	(Galsworthy et al. 2023)
**Hyposoter seniculus* (Gravenhorst, 1829)	MZL, NMB	
**Hyposoter sicarius* (Gravenhorst, 1829)	MZL, NMB	
**Hyposoter tibialis* (Hedwig, 1938)	MZL, NMB	
**Hyposoter tricolor* (Ratzeburg, 1844)	MZL	
**Hyposoter tricoloripes* Viereck, 1911	MZL, NMB	
**Hyposoter validus* (Pfankuch, 1921)	MZL, NMB	
**Hyposoter virginalis* (Gravenhorst, 1829)	MZL, NMB	
**Hyposoter vividus* (Holmgren, 1860)	MZL, NMB, NMBE	

and *H. seniculus* (Fig. 3). The latest collected specimen belongs to *H. praecaedator* and was collected on November 8, 2023 in Lucerne. Specimens of many species were recorded until mid-October (Fig. 3). In general, it appears that more specimens were collected in the second half of the year, although with a large gap between 1,000 and 1,500 m elevation after August (Suppl. material 2).

Several species are clearly either bivoltine or plurivoltine since they appear over a long period and show at least two separate clusters in their collection dates, for example, *H. dolosus* (early June and early August) and *H. caedator*

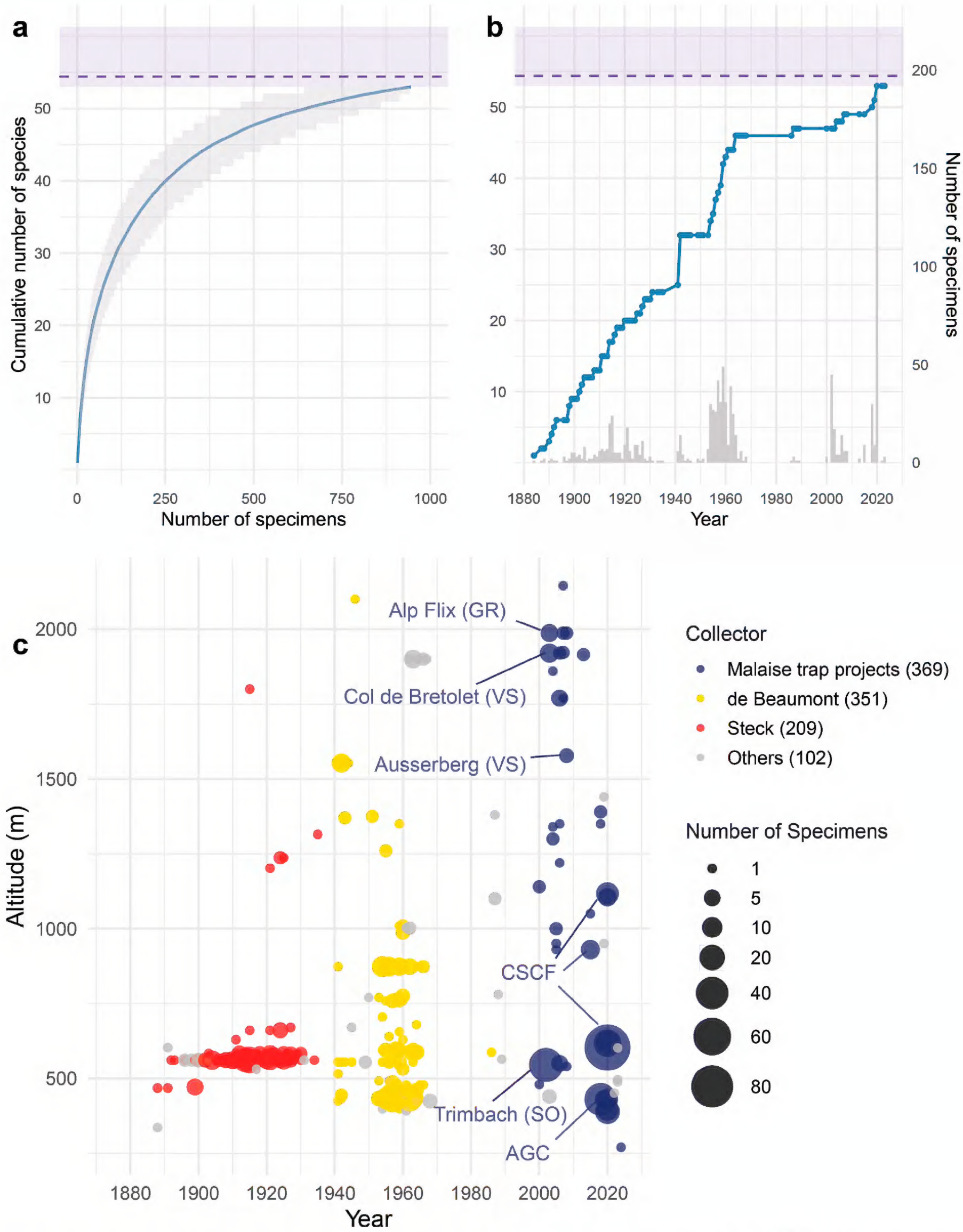

Figure 1. Species accumulation curves and collection history of *Hyposoter* species (N = 53) in Switzerland: **a.** Specimen-based species accumulation curve; variance calculated using 1,000 random iterations (95% CI, shown in grey). The result of the abundance-based coverage estimator (54.4) is shown as a violet dashed line with the 95% CI (53.0–61.3) as violet transparent area. **b.** Cumulative number of species versus year (blue curve, corresponding with the y-axis on the left side); specimens collected per year are indicated as grey bars, corresponding with the y-axis on the right side. Note the large number of specimens collected by Malaise traps in the most recent years. **c.** Altitudinal distribution of *Hyposoter* specimens in Switzerland plotted against the year of the record. The records are scaled in size by the number of specimens recorded in the same year and at the same altitude. Material collected by the most prolific collectors (Theodor Steck and Jacques de Beaumont) and by Malaise trap projects are shown in different colours. Some of the larger Malaise trap projects are annotated within the plot. CSCF = Centre Suisse de cartographie de la Fauna; AGC = L'Association de la Grande Cariçaie.

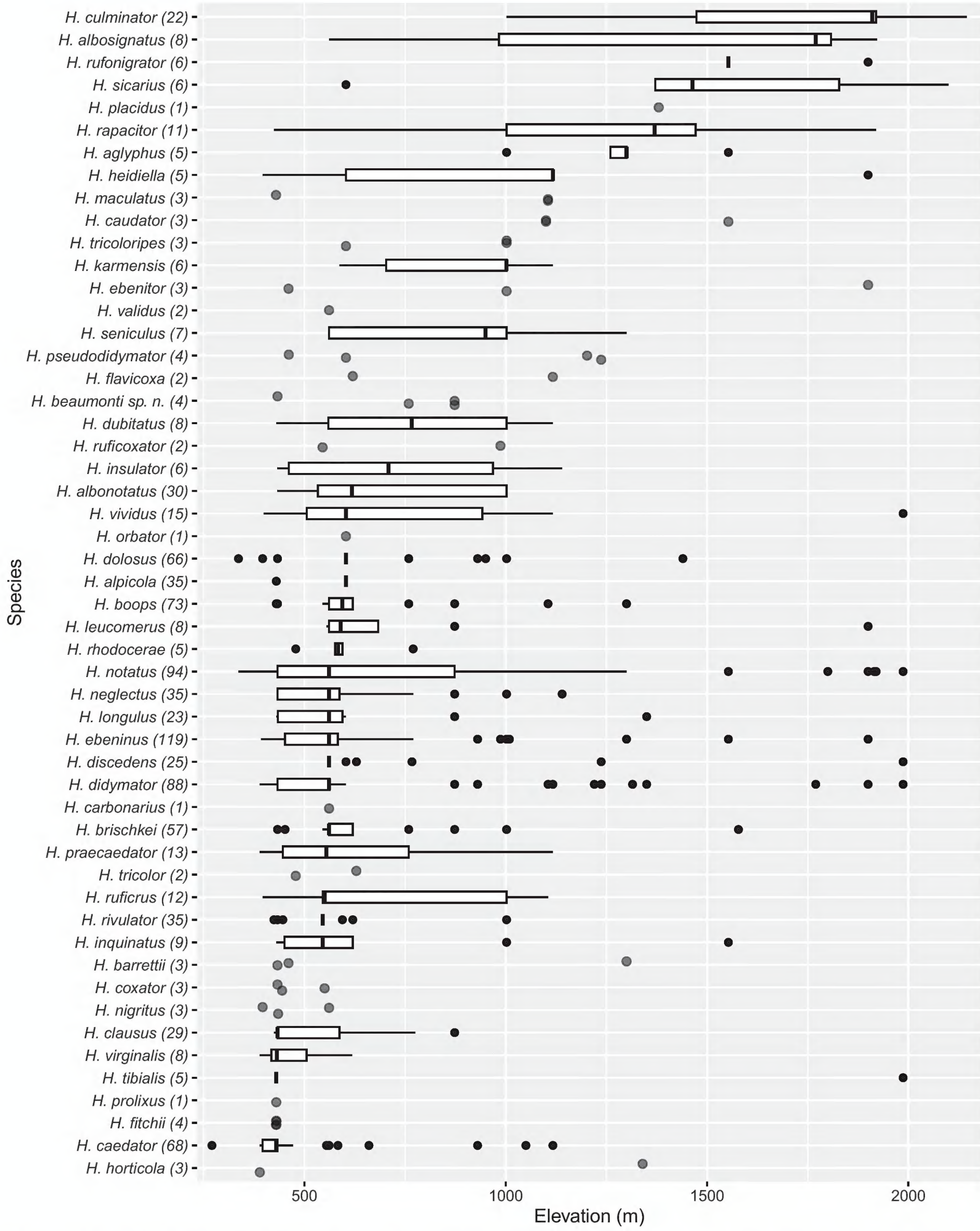

Figure 2. Altitudinal distribution of *Hyposoter* species in Switzerland based on locality information from specimens in Swiss natural history collections. Species are sorted based on their median altitude in our records. The number of specimens is shown in brackets behind the species name (N = 984). Species represented by less than five specimens are shown as dots instead of boxplots. Species with an interquartile range of 0 (Q1 = median = Q3), only the median (vertical line) of the boxplot and outliers are visible.

(late June and late August). In general, we would assume that all species with a collection span of more than three months are likely plurivoltine (Fig. 3). Some species appear for up to half a year, for example, *H. didymator*, *H. notatus* (both early April until early October), or *H. ebeninus* (early May until mid-October). In contrast, it is difficult to

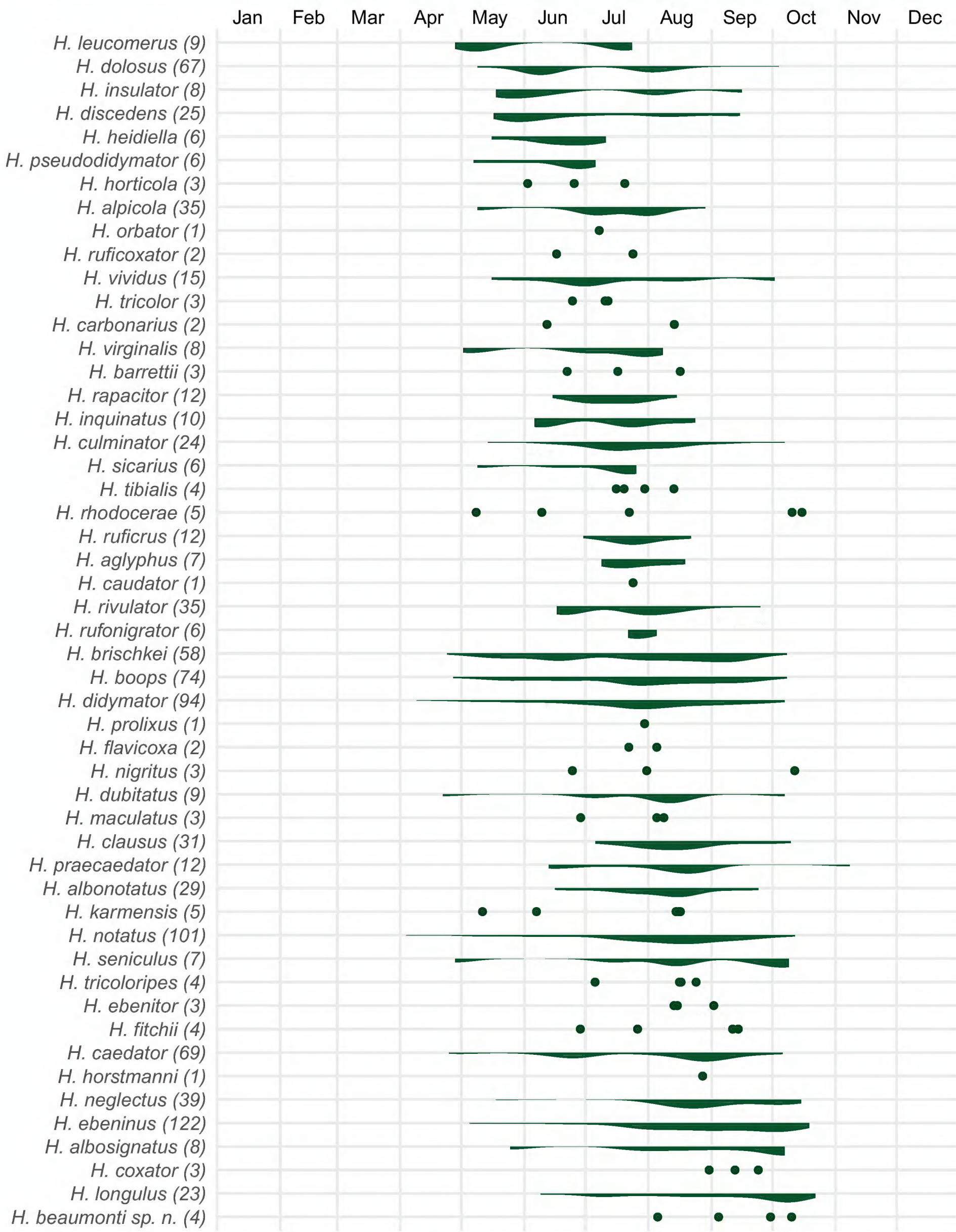

Figure 3. Phenology of *Hyposoter* species in Switzerland based on collection date recorded for specimens in Swiss natural history collections. The number of specimens is shown in brackets behind the species name (N = 1,024). Species are sorted in order of their median collection date. Species represented by five or less specimens are shown as dots instead of half-violins. Dots are jittered randomly by +- 3 days to show overlapping data points.

be sure when a species is univoltine, since it could simply be due to data deficiency. However, there are a couple of species with at least 10 specimens collected individually that appear only within 1–2 months, for example, *H. ruficrus* (early July until mid-August) or *H. rapacitor* (mid-June until mid-August).

Novel host records

We provide so far unpublished host records for five *Hyposoter* species and specimens reared in Switzerland. Verbatim label data is available in Suppl. material 1 and Zenodo (https://doi.org/10.5281/zenodo.17858878).

Hyposoter barrettii (Bridgman, 1881)

One female of *Hyposoter barrettii* (NMB-HYME-NO0007134, NMB) was reared from the Pterophorid *Oxyptilus tristis* (Zeller, 1841), which was collected in Törbel (VS) on *Hieracium amplexicaule* L. by Jürg Schmid and emerged on April 28, 2019 (code: 01i11). *H. barrettii* appears to be specialized on Pterophoridae, since it was already reared from various other species from this moth family (Shaw et al. 2016).

Hyposoter didymator (Thunberg, 1824)

One female of *Hyposoter didymator* (GBIFCH 02037695, NMBE) was reared from the noctuid *Lacanobia aliena* (Hübner, 1808/1809), which was collected in La Neuveville (BE) on *Aster linosyris* (L.) by R. Bryner on July 17, 1989, and emerged on August 13 (code: 01111). *H. didymator* was previously reared from various other Noctuidae, but also Geometridae, Lasiocampidae, Nymphalidae, Notodontidae, Papilionidae and Pieridae across Europe (Shaw et al. 2016).

Hyposoter dolosus (Gravenhorst, 1829)

One female of *Hyposoter dolosus* (GBIFCH 02037707, NMBE) was reared from the erebid *Spiris striata* (L.) by P. Marmet, unfortunately without locality data, collection date, nor host remains (code: 01011). *H. dolosus* has previously been reared from *S. striata* and several other erebids across Europe (Shaw et al. 2016).

Hyposoter placidus (Desvignes, 1856)

One female of *Hyposoter placidus* (GBIFCH 02037972, MZL) was reared from *Lycaena hippothoe* (Linnaeus 1761), which was collected in Ollon (VD) by R. Bryner on June 5, 1987, and emerged on June 25 (code: 01111). *H. placidus* was previously reared from *L. hippothoe* in Andorra and Spain and from various other *Lycaena* spp. in Europe (Shaw et al. 2016).

Hyposoter validus (Pfankuch, 1921) (uncertain)

One male specimen which matches *Hyposoter validus* very well (NMB-HYMEN0002601, NMB) is annotated with the labels "D. pini", "BERN", "IX III 31". Although identification of this male is somewhat uncertain, because males of this species have not previously been seen by any of us, we decided to report this record here, as only a single host record is available for the species (see below).

We interpret the label data to indicate that this specimen was reared from the lasiocampid *Dendrolimus pini* (L.), collected in Bern and probably emerged on March 9, 1931. The collector is not known, and no host remains are present with the specimen (record value: 0i011). There is some support for this host record, since *H. validus* has previously been reported from *Dendrolimus sibiricus* (Tschetverikov, 1908), a record that also needs further verification according to Galsworthy et al. (2023).

Description of new species

Hyposoter beaumonti sp. nov.

https://zoobank.org/8965D246-ACC8-4597-AAE1-F55D6C74D998

Fig. 4

Material examined. ***Holotype.*** • 1 ♀, Switzerland Vaud, Jorat, Ste. Catherine, leg. Jacques de Beaumont, 1962-X-02, GBIFCH 02039264 (MZL). ***Paratypes.*** • 1 ♀, same data as holotype, except 1955-X-08, GBIFCH 02039265 (MZL). • 1 ♀, Neuchâtel, Rochefort, La Tourne, leg. Jacques de Beaumont, 1959-VIII-06, GBIFCH 02039266 (MZL). • 1 ♀, Neuchâtel, Milvignes, Auvernier, leg. Jacques de Beaumont, 1955-IX-03, GBIFCH 02039267 (MZL).

All type material is deposited at the Naturéum, Muséum cantonal des sciences naturelles, Lausanne (MZL).

Diagnosis. This species can be differentiated from all other Western Palaearctic *Hyposoter* species by the following character combination (order follows the key (Galsworthy et al. 2023)): metasomal tergites dark brown to black, with narrow yellow posterior rims; tegula yellow; all coxae black, fore and mid coxae marked with yellow proximally; hind femur dark brown to black; clypeus and genae black; metasomal sternites marked with black; hind tibia dark brown to black basally and apically, yellow to orange medially, without basal white spot; first tarsomere of hind leg dark brown to black with very narrow yellow basal ring; ovipositor very short, its sheaths hardly protruding from apex of metasoma.

Hyposoter beaumonti sp. n. runs in the key for Western Palaearctic *Hyposoter* (Galsworthy et al. 2023) to couplet #14. It differs from *H. tricolor* (Ratzeburg, 1844) and *H. albonotatus* (Bridgman, 1889) by the first tarsomere of the hind leg being dark brown to black with a narrow yellow basal ring instead of pale orange (*H. tricolor*) or white with a distal black quarter (*H. albonotatus*). From *H. tricoloripes* (Viereck, 1911), *H. beaumonti* can be differentiated by the lack of a basal white spot on the hind tibia (present in *H. tricoloripes*). The hypervariable *H. caedator* (Gravenhorst, 1829), especially the dark forms (formerly *H. caedator corsicator* Aubert, 1960), is also somewhat similar to *H. beaumonti*, but clearly differs by the lighter coloured trochanters, hind femur and metasomal tergites, and the narrower area superomedia (1.2–1.4 × as long as wide; compared to 0.8–1.2 × in *H. beaumonti*; see also Suppl. material 3).

Description. Female (measurements of holotype in brackets).

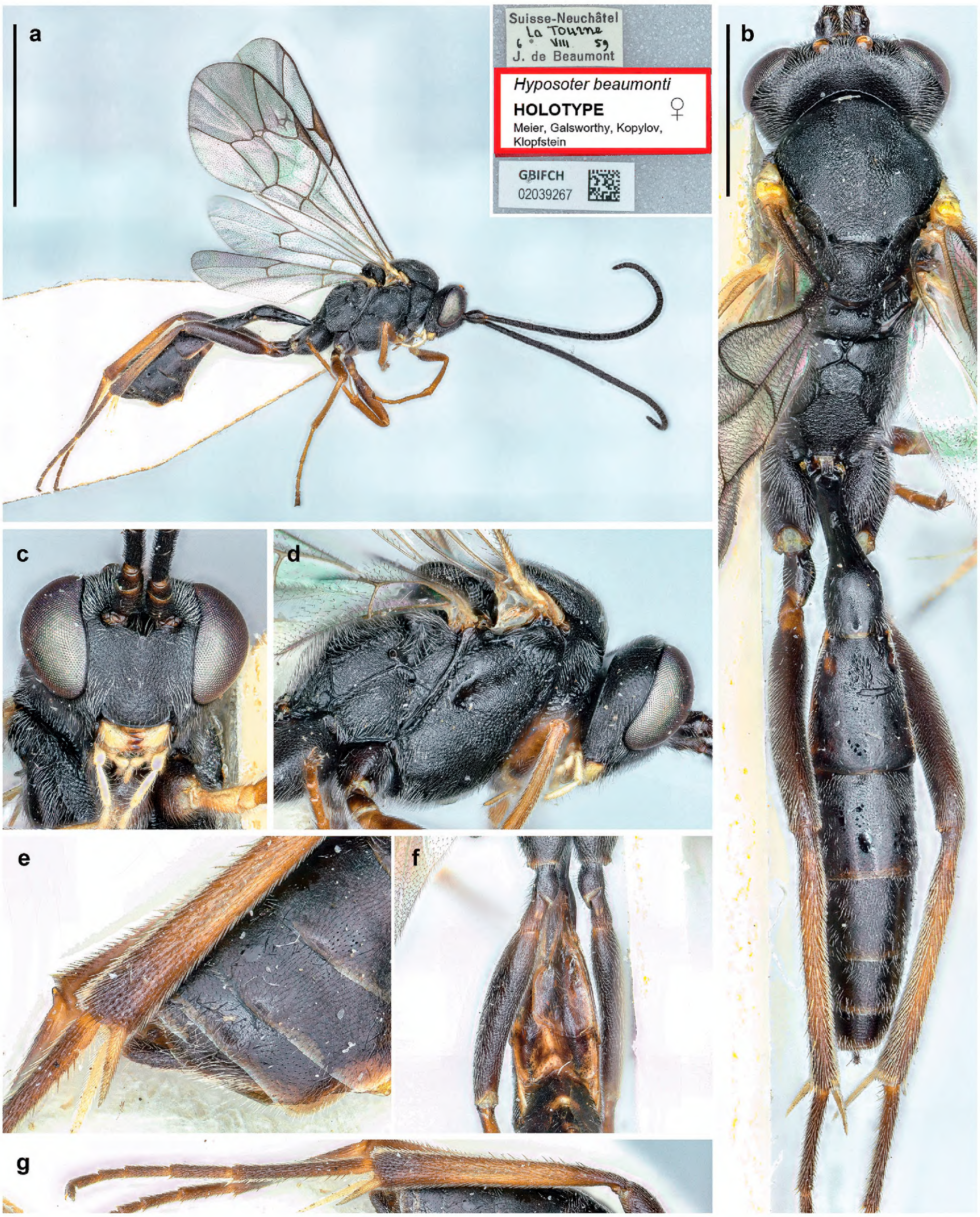

Figure 4. *Hyposoter beaumonti* sp. nov. holotype female: **a.** Habitus lateral view with labels as inset picture; **b.** Habitus dorsal view; **c.** Face frontal view; **d.** Head and mesosoma lateral view; **e.** Apex of metasoma; **f.** Metasomal sternites 1–3; **g.** Hind leg. Scale bars: 3 mm (**a**); 1 mm (**b**).

Head. Face 2.0–2.1 × (2.0×) wider than high, coriaceous; inner margins of eyes slightly converging. Distance between posterior ocelli 1.3–1.6 × (1.6×) diameter of posterior ocellus; distance between posterior ocelli and margin of compound eye 1.2–1.3 × (1.3×) diameter of one posterior ocellus. Clypeus 1.5–1.8 × (1.7×) wider than high, moderately convex, coriaceous with weak punctation; malar space 0.8–1.0 × (0.8×) base of mandible. Frons, vertex and temple coriaceous. Occipital carina joining hypostomal carina about 0.4–0.5 × (0.4×) as far from base of

mandible as its width at base. Mandibular flange distinct from mandibular base to base of mandibular teeth, about as wide as one mandibular tooth. Antenna slender, slightly tapered in apical half; with 31–32 (31) flagellomeres, penultimate flagellomere 1.1–1.6 × (1.1×) as long as wide.

Mesosoma. Moderately elongate. Pronotum, mesopleuron, metapleuron, mesoscutum and scutellum coriaceous and dull; speculum finely coriaceous and shining. Propodeum with carination well developed, lateral part of anterior transverse carina ("costula") indicated but incomplete laterally; coriaceous with some transverse wrinkles in area petiolaris. Area basalis rather short, triangular with an apical stalk of about the same length as the area itself; area superomedia 0.8–1.2 × (0.8×) as long as its maximum width, posteriorly open but with transverse rugae in area petiolaris at times nearly closing it (especially in one paratype).

Wings. Fore wing 4.9–5.4 mm (4.9 mm); vein 1*cu-a* postfurcal; areolet petiolate. Hind wing with nervellus slightly curved.

Legs. Inner hind tibial spur 0.6 × (0.6×) as long as first hind tarsomere; fore and hind tibiae densely setose with some distinctly thickened setae.

Metasoma. Tergite 1 with a distinct glymma closer to spiracle than to anterior end of tergite; laterally smooth and shining anterior to glymma, postpetiolus dorsally coriaceous and dull. Remaining tergites coriaceous and dull; tergite 2 with thyridium elongate, elliptical. Ovipositor sheath 0.1–0.2 × (0.2×) as long as hind tibia, hardly protruding beyond apex of metasoma.

Colour. Black; mandibles, palps and tegulae yellow. Fore and mid legs with coxae distally yellow, trochanters yellow ventrally and apically, trochantelli completely yellow, femora orange, marked black proximally, tibiae and tarsi yellow to orange; hind leg with coxa black, marked with light brown distally, trochanter and trochantellus dark brown to black, marked with pale brown to orange distally, femur dark brown to black, marked with pale brown proximally, tibia yellow to orange, with dark brown to black markings at base and apex, tarsus dark brown to black; tibial spurs ivory. Metasomal tergites dark brown to black with narrow pale brown apical rims; sternites mostly dark brown or black.

Male: unknown.

Biology. unknown.

Etymology. Dedicated to Jacques de Beaumont (1901–1985), a former curator and director of the cantonal museum of Zoology (today the Naturéum - Muséum cantonal des sciences naturelles) and professor at the University of Lausanne. He was the single most prolific collector of *Hyposoter* specimens in Switzerland.

Taxonomic remarks

Hyposoter caedator corsicator Aubert, 1960

Hyposoter caedator corsicator Aubert, 1960 was described as a subspecies restricted to Corsica. The only diagnostic characters differentiating it from *H. caedator* (Gravenhorst, 1829) are its darker metasomal colour and the brown to black hind tibia (Aubert 1960). We studied the type series of *H. c. corsicator* consisting of 27 syntypes (MZL) and found a lot of variation among the syntype series with regard to both diagnostic characters. Furthermore, specimens of *H. caedator* collected from the same localities in Switzerland (current manuscript) and in Spain (Horstmann collection, ZSM; Galsworthy et al. 2023) vary strongly in the extent of orange metasomal coloration (Suppl. material 3). Since these colour variants show a sympatric distribution, and we could find no structural characters that could distinguish the specimens from Corsica from the ones from the continent, they do neither qualify as subspecies, nor is there enough evidence to raise them to the level of species. For these reasons, we formally synonymize *Hyposoter caedator corsicator* Aubert, 1960 with *Hyposoter caedator* (Gravenhorst, 1829) (syn. nov.).

Hyposoter castaneus Galsworthy & Shaw, 2023

On further study of the morphology, we have come to the conclusion that *Hyposoter castaneus* is a junior synonym of *Lemophagus curtus* Townes, 1965, and therefore formally designate it as such (syn. nov.). We have studied the holotype of *H. castaneus*, specimens of *L. curtus* held in the NHMUK, including one paratype, and specimens of *L. curtus* identified by Klaus Horstmann (Bass and Bennett in prep.). Morphological characters of the species align with the genus description of *Lemophagus*: broad clypeus and face, both with rugulose sculpture; mesopleuron with clear transverse rugae in front of a smooth speculum (Horstmann 2004; Klopfstein et al. 2022). The presence of the glymma varies in specimens formerly identified as *H. castaneus* from being completely absent to a faint suggestion as a weak groove, suggesting that the presence or absence of a glymma is not the best character to differentiate the species from other congeners, e.g. *L. crioceritor* Aubert, 1986 (Horstmann 2004).

Hyposoter monensis Galsworthy & Shaw, 2023

Having studied both holotypes (Suppl. material 4), we found that *Hyposoter monensis* is a junior synonym of *Phobocampe nigra* Šedivý, 2004. Morphological characters of the species indicate that it should belong in *Hyposoter* rather than *Phobocampe*: angle between 1cu-a and 2Cu in forewing about 80° (usually below 60° in *Phobocampe*), eyes parallel (not converging), hind wing vein M+Cu for a relatively long distance parallel with 1A, with bow relatively far away from the junction with 1Cu and cu-a (see other diagnostic characters in (Klopfstein et al. 2022).

In consequence, the senior synonym *Hyposoter niger* (Šedivý, 2004) becomes a secondary homonym of *Hyposoter niger* (Brullé, 1846). Following Article 23.3.5 of the International Code of Zoological Nomenclature (ICZN), *Hyposoter monensis*, as the only junior synonym remains the valid name of this species.

Corrigendum to Galsworthy et al. 2023

It has become apparent that the photographs used to illustrate *Hyposoter meridionellator* Aubert 1965 in couplet 71 of the key in Galsworthy et al. 2023 were not of that species, but of a misidentified specimen of *Lemophagus pulcher* Szepligeti, 1916 (Bass and Bennett in prep.). Some of the characters from this specimen were transferred into the couplet, and are not consistent with the holotype of *H. meridionellator*. The couplet should therefore be revised to:

71 Petiole without glymma ..... *H. meridionellator* Aubert, 1965 ♀
-Petiole with obvious glymma 72

Discussion

Where did these 46 unrecorded species hide?

Reporting several dozen species as new for a country in the middle of Europe might be surprising at first glance. However, this situation is actually not that unusual for parasitoid wasps, which belong to the so-called "dark taxa", mostly due to historical neglect (Page 2016; Klopfstein et al. 2019b). The checklist of Darwin wasps in Switzerland (Klopfstein et al. 2019a) was constructed with a very conservative approach, only including material identified by specialists for the group. For about seven additional *Hyposoter* species, there were previously identified specimens in the Swiss collections, but as these originated from before a time when *Hyposoter* specimens could be reliably identified, these were ignored in the previous checklist. We were able to confirm that *H. dolosus*, *H. carbonarius* (under the synonym *H. pectinatus* (Thomson, 1887)), *H. leucomerus* and *H. notatus* were correctly identified by Sigismund Brauns. *H. neglectus*, although recorded here from Switzerland, was probably confused by Brauns with *H. boops*. Specimens determined by Charles Ferrière (*H. notatus*, *H. sicarius*, *H. ebeninus*) are stored in the natural history collections in Chur and Geneva and were not studied here.

The largest quantity of *Hyposoter* specimens in Switzerland were collected many decades ago, mostly by Theodor Steck and Jacques de Beaumont, but simply remained unidentified in the collections up until this study (Fig. 1b). Even though de Beaumont was working after Steck, he collected a larger number of new *Hyposoter* species per year in Switzerland. This pattern can only in part be explained by de Beaumont's greater sampling intensity – the more important factor was clearly the more heterogeneous collecting localities he visited, including sites across a broader elevational range (Fig. 1c, Suppl. material 1). After his remarkable efforts, it is only thanks to strongly increased sample sizes between 2000–2020 that additional species of *Hyposoter* have been recorded (Fig. 1c). Interestingly, most of these were Malaise trap projects primarily focused on Syrphid flies or non-ichneumonid parasitoid wasps. It was only because all by-catch (i.e., non-target insects) were sorted to at least order or family level that they could be included in this study. This highlights the high value of by-catch material and underscores the importance of properly processing and making it accessible to specialists (Spears and Ramirez 2015; Urfer et al. 2025).

Despite the varying collecting effort over time, the discovery of 47 so far unrecorded species of *Hyposoter* in Switzerland is principally due to extensive efforts at species identification (N = 46) and new species description (N = 1) as part of this study. Reliable identification in *Hyposoter* has only recently become feasible, following the systematic review of Western Palaearctic species by Galsworthy et al. (2023), highlighting the critical role of taxonomic revision and robust identification keys. We further emphasize that the digitization of natural history collections represents a crucial next step following reliable species identification, as it facilitates subsequent faunistic and ecological analyses.

Where do we expect to find even more unrecorded *Hyposoter*?

Covering the major Darwin wasp collections in Switzerland, we have here recorded 53 out of the 71 known Western Palaearctic *Hyposoter* species in Switzerland (Galsworthy et al. 2023), which is already a lot compared to the checklists for other well-studied countries, such as Germany (N = 42; Riedel et al. 2021; Galsworthy et al. 2023; corrected with this study) and the United Kingdom (N = 35; Broad 2016; Galsworthy et al. 2023; corrected with this study). According to the species richness estimation based on our sample, we can expect between 54–61 species (ACE, 95% CI). This means that Switzerland might harbour 76–87% of the Western Palaearctic species, which is comparable to the percentage of other well-studied ichneumonid groups such as Diplazontinae with 74% (99 species in Western Palaearctic, Klopfstein 2014; 73 species in Switzerland, Klopfstein et al. 2019a). However, it is a much higher percentage than, for instance, in aculeate hymenopterans such as bees, where Switzerland hosts less than 30% (632 species in Switzerland and 2,130 species in Europe, Praz et al. 2023), or other insect groups (Neumeyer 2019; Cosandey et al. 2024). Chao-I and ACE are useful tools to account for rare species that have not yet been sampled within study sites. However, there might well be further habitat types that have been heavily under-sampled or have not yet been sampled at all, and which species-richness estimators cannot yet account for. For future sampling projects,

we encourage targeted over quantitative sampling, with the inference that sampling localities should be stratified into altitudinal gradients or habitat types. Good examples of such sampling approaches are the Malaise trap projects by the CSCF and AGC projects which sampled in rare habitats, or by the NMBE and the NMB which often targeted localities at higher elevations, which had only rarely been sampled before (Klopfstein et al. 2019a).

Taxonomic work with *Hyposoter* is still ongoing (Galsworthy et al. 2023, this study here). Recently collected material of undescribed species as well as undescribed morphospecies in natural history collections suggest that plenty of further species still await taxonomic description (pers. comm. Håkon Haraldseide, Andrew Bennett). Further taxonomic changes can also be expected at the generic level, once phylogenetic analyses hopefully help to further clarify the genus borders within the *Diadegma* genus group (Klopfstein et al. 2022). Within *Hyposoter*, this could affect the generic placement of species which stand very close to *Olesicampe*, such as *H. discedens* (Galsworthy et al. 2023), and a number of species resembling some *Diadegma* or *Tranosemella*. As we show in this study, misidentifications of *Hyposoter* species might even include genera outside the *Diadegma* genus group, as in the case of *Phobocampe nigra* and *Lemophagus curtus*.

Altitudinal patterns in *Hyposoter* Darwin wasps

We found that *Hyposoter* is most diverse at low elevation in Switzerland, with only three species appearing to be high-elevation specialists (Fig. 1; Suppl. material 5). Of these, *H. culminator* and *H. rufonigrator* were already described as montane species (Galsworthy et al. 2023). More surprisingly, *Hyposoter albosignatus*—described from Northern Wales at < 100 m elevation (Galsworthy et al. 2023)—exhibits a median altitude in Switzerland of > 1,750 m. Further data on its distribution and biology are needed to clarify this pattern. Among additional montane *Hyposoter* species (Galsworthy et al. 2023), we find *H. alpicola* with a median altitude of 700 m, and there are no confirmed records of *H. nigromaculatus* (Strobl, 1904) in Switzerland so far.

The reported diversity peak at low elevation for *Hyposoter* contrasts with the distribution patterns of other Darwin wasps in the Western Palaearctic (Schwarz 2002; Klopfstein et al. 2007). In Austria, for example, 9% of the country's Darwin wasp species have been collected above the tree line in the Hohe Tauern (Schwarz 2002). For Diplazontinae, 38% of Western Palaearctic species have been recorded from a single high-elevation study site in Switzerland (1,680–1,980 m) (Klopfstein et al. 2007). In Diplazontinae, this pattern is likely driven by the distribution of Syrphidae hosts (Klopfstein et al. 2007). The lepidopteran hosts of *Hyposoter* (notably Noctuidae and Geometridae) show a similar pattern of higher diversity at low elevations in spring and autumn, with a shift to mid-elevation diversity peaks in summer (Beck et al. 2010). For *Hyposoter*, we did not observe such a seasonal shift in the altitude of peak diversity (Suppl. material 5). Whether other campoplegine genera show a pattern analogous to *Hyposoter* remains to be tested. If host distribution largely determines the pattern, the subfamily could be quite heterogeneous due to the diversity of host groups.

Nevertheless, we think that montane habitats are of importance for many species (not only specialists), due to the prevalence of low-intensity management that might create a refuge for species under pressure in the intensively managed low elevation plateau (Marini et al. 2009). In addition, montane habitats harbour unique habitat types, some of which have been largely destroyed in the agricultural landscape, such as raised bogs (Grünig et al. 1986). Today, 70% of Switzerland's raised bogs are found at altitudes between 850 and 1450 m elevation, whereas they were originally much more widespread across the lowland plateau, where they have since suffered extensive destruction (Grünig et al. 1986). It is also possible that montane habitats are becoming more intensively used by cold-adapted species which are coming under pressure due to changing climate (Wilson et al. 2005; Chen et al. 2011; Elsen and Tingley 2015; Steinbauer et al. 2018). However, due to large gaps in our data on the time axis for most species, these data are not sufficient to evaluate whether species have changed their altitudinal distribution over time. In summary, these results indicate that montane habitats in Switzerland provide suitable habitats for nearly half the species of *Hyposoter*, and perhaps for some even the only suitable habitats.

Author contributions

Conceptualization: NM, AG, DK, SK. Data curation: NM. Funding acquisition: NM, SK. Investigation: NM, AG, DK, SK. Methodology: NM, SK. Project administration: NM, SK. Supervision: SK. Validation: AG, SK. Visualization: NM, DK, SK. Writing - original draft: NM. Writing - review and editing: NM, AG, DK, SK.

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Supplementary material 1

Collection data of 1,046 specimens of *Hyposoter* from Switzerland

Authors: Noah Meier, Anthony Galsworthy, Dmitry Kopylov, Seraina Klopfstein

Data type: csv

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Link: https://doi.org/10.3897/alpento.10.175647.suppl1

Supplementary material 2

Comparison in the species accumulation curves between the two collectors Theodor Steck and Jacques de Beaumont

Authors: Noah Meier, Anthony Galsworthy, Dmitry Kopylov, Seraina Klopfstein

Data type: pdf

Explanation note: The species accumulations curves (blue and red inner lines) and the 95% CI (grey area) are calculated using 1,000 iterations of random shuffling of the specimens' order.

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Link: https://doi.org/10.3897/alpento.10.175647.suppl2

Supplementary material 3

Different morphotypes of *Hyposoter caedator* (Gravenhorst, 1829)

Authors: Noah Meier, Anthony Galsworthy, Dmitry Kopylov, Seraina Klopfstein

Data type: png

Explanation note: **a–c.** Syntype (1/27) of *H. caedator corsicator* Aubert, 1960. **d–f.** Dark morphotype matching specimens labelled as *H. caedator corsicator* and *H. caedator* forma osbcura in the Aubert collection. **g–i.** median morphotype matching specimens labelled as *H. caedator* forma henscheli in the Aubert collection. **j–l.** Light morphotype matching specimens labelled as *H. caedator* in the Aubert collection. left column. habitus, with inset image showing labels. center column. face, anterior view. right column. propodeum, dorsal view. Scale 1 mm.

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Link: https://doi.org/10.3897/alpento.10.175647.suppl3

Supplementary material 4

Phobocampe nigra Sedivy, 2004 holotype female

Authors: Noah Meier, Anthony Galsworthy, Dmitry Kopylov, Seraina Klopfstein

Data type: png

Explanation note: Horstmann Collection, Zoologische Staatssammlung München (ZSM). **a.** Habitus in lateral view, labels as inset picture; **b.** Habitus in dorsal view; **c.** Face; **d.** Cocoon; **e.** Wings. Scale 1 mm (**a, b**).

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Link: https://doi.org/10.3897/alpento.10.175647.suppl4

Supplementary material 5

Hyposoter specimens in collections are most abundant and species rich from lower altitudes and mid-summer months

Authors: Noah Meier, Anthony Galsworthy, Dmitry Kopylov, Seraina Klopfstein

Data type: pdf

Explanation note: Heatmap grid showing abundance and species richness on the time of year versus altitude axes.

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